BREVIORA

THE EVOLUTION OF BEHAVIOR
AND THE ROLE OF BEHAVIOR IN EVOLUTION

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ABSTRACT. Modern behavior studies are, or should be, primarily concerned with problems of causation. The immediate causes of particular behavior patterns are being analyzed at the physiological and biochemical levels. The ultimate causes, selection pressures, are being studied by ecologists and ethologists. Unfortunately, there is little contact between the two lines of investigation at the moment. Doubtless a new synthesis will be achieved in the future. It does not, however, appear to be imminent. In the meantime, the results of behavior studies in the field or in the laboratory in semi-natural conditions can still be of use to the evolutionary biologist. They may be most helpful in revealing the details, mechanics, of certain ecological processes, which are themselves the regulators or determinants of evolutionary events. Some examples from recent work on cephalopods, monkeys, and birds may illustrate the sorts of data that are both available and relevant.

INTRODUCTION

I have been asked to talk about my own work on animal behavior and related subjects, and also to say something about possible further developments of behavioral studies in general. The prospect of thus anticipating the future is not entirely gratifying. It seems to me that current research on animal behavior has reached a difficult, awkward, almost embarrassing stage. As is the case with any subject, there are numerous false starts and unrewarding pursuits. Some questions being asked by workers in the field are hardly worth posing. The answers are self-evident or easily predictable. Some other questions are devoted to more significant problems, but apparently cannot be answered with the techniques currently available, at least not the techniques actually being used. More important, the various kinds

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of studies that are proving to be useful and successful are becoming increasingly disparate in both methods and objectives.

This anomalous situation is, of course, the result of historical factors. It might be instructive, therefore, to give a brief résumé of some aspects of the past, in order to explain the present unease and to provide or reveal a reasonable rationale for some of the continuing work — my own included.

Many biologists, the majority of evolutionary biologists and "natural historians," probably would agree that the most stimulating school of behaviorists in this century was that of the "ethologists." Ethology as such may be difficult to define. In theory, the term could be applied (without paying too much attention to its classical derivation) to the whole of the science of behavior. In fact, it is usually restricted to a particular approach to the subject, based upon Darwin (1872) and other pioneers such as Heinroth (1911), Whitman (1899 and 1919), Huxley (1914), and Craig (1918), and perhaps influenced by some early ideas of Freud or his predecessors, but largely developed in continental or Teutonic Europe in the 1930's and 1940's and subsequently widely diffused, first in the English-speaking world and then elsewhere in the next decade.

This school was distinguished by a concentration upon large segments or sequences of behavior in natural or semi-natural conditions, especially social (inter-individual behavior and the reactions that were called at the time "innate," *i.e.*, species-typical or (often by implication) species-specific. Among the better known products of the school which may serve to illustrate its original range of interests were papers by Lorenz (*e.g.*, 1931, 1935, 1941), Lorenz and N. Tinbergen (1938), N. Tinbergen (1932, 1935, 1936, 1939, 1940), Makkink (1936), Kortlandt (1940), Seitz (1940 and 1941), and Baerends and Baerends (1950).

Another characteristic of the first ethological studies was a preoccupation with causes, not only long-term components such as selection pressures affecting behavior in the course of evolution but also short-term or even immediate causes, external and internal states and stimuli and internal mechanisms producing particular acts at particular instants in time. The latter interest entailed a considerable amount of rather ambitious and detailed model-building, the development of concepts and terms such as "Innate Releasing Mechanism," "reaction specific energy," "displacement" activities, and "hierarchies" of instincts. The state of the art at this stage is beautifully summarized in N. Tinbergen

(1951). Unfortunately, most of the models proved to be descriptive of the overt manifestations of behavior but not explanatory or usefully predictive. They did not correspond very closely to the actual events within a behaving animal. (This sort of discrepancy between the perceived and the real is an occupational hazard of model-building. There may be comparable gaps in ecological models — a topic that will be mentioned later.)

The responses of ethologists to their logical and methodological difficulties were exceedingly diverse:

1. The original mainstream of effort was impeded and reduced but did not dry up completely. There were hopeful and ingenuous attempts to redefine and refine the classic concepts (see, for instance, Bastock *et al.*, 1953; Hinde, 1954a and 1954b; Morris, 1957; Blest, 1961). Some of these attempts may have been helpful in minor ways, but I think that it would be fair to say that they did not do very much to resolve the basic dilemma. There was a push to render descriptions more precise, by adoption of mathematical and pseudo-mathematical means of notation, often with an infusion of information theory and cybernetic terminology, and by increased use of improved photographic and other kinds of recording equipment. Examples are too numerous to cite, but many can be found in recent issues of the journals "Behaviour" and "Animal Behaviour" and the bibliographies of the general surveys of Hinde (1970), Eibl-Eibesfeldt (1970), and Marler and Hamilton (1967). All too often, they have merely told us what we already knew or assumed, at distressingly greater length and elaboration than we were prepared to cope with.

2. Perhaps a more practical response was switching of attention to groups of animals and special problems that had been neglected in earlier years. Several bends in the river or new channels which are in some danger of becoming oxbows but are at least picturesque. There has been a great deal of strictly ethological work on a variety of "lower" mammals such as marsupials, rodents, and carnivores (*e.g.*, Kaufmann, in press; Kleiman, 1972; Leyhausen, 1956; Kruuk, 1972; Schaller, 1972; Ewer, 1963, 1968, and 1973), and an enormous proliferation of studies and surveys of primates (*e.g.*, Altmann, 1967; Chance and Jolly, 1970; Crook, 1970; DeVore, 1965; Dolhinow, 1972; Imanishi and Altmann, 1965; Jay, 1968; Jolly, 1966 and 1972; Kummer, 1968 and 1971; van Lawick-Goodall, 1971; Morris, 1967a; Moynihan, in press a; Petter, 1962; Poirier, 1972; Reynolds, 1968; Rosenblum and Cooper, 1968; Rowell, 1972;

Schaller, 1963; Struhsaker, 1969). Many of these papers were indirect reflections of a strong interest in human behavior, both as it is and as it may be supposed to have been at some earlier time in the Pliocene or Pleistocene; and there have also been attempts to apply conventional ethological insights to some of the urgent problems of modern man (*e.g.*, Lorenz, 1963; Russell and Russell, 1968; Morris, 1967b; Martin, 1972) with amusing results (critics have tended to dismiss both the good and bad suggestions and interpretations as impertinent *sensu stricto,* but it may be hoped that some of them will eventually be incorporated into the intellectual background of the well-informed citizen).

The most fashionable of the special subjects has been what might be broadly called "communication." Different aspects of the subject have been tackled at many different levels and in many different areas. There have been analyses of the various ways in which information, true or false, can be transmitted among individuals of the same or different species, and also of the means by which transmission can be prevented or interrupted. One of the aspects of interspecific communication that has attracted investigation and speculation is mimicry, not only the long known Batesian and Mullerian types but also aggressive and social and even more recondite forms. Relevant publications include Brower *et al.* (1960, and many other papers from the same school); Rand (1967); Robinson (1969); Moynihan (in press b), and an extensive discussion and summary in Wickler (1968). The methods by which predators discover and recognize prey, with or without the baffles of mimicry and crypsis, have been studied by many workers. The papers of Robinson and his collaborators (*e.g.,* 1969, 1971a, 1971b) reveal some of the factors that may come into play. Research on intra-specific communication has been primarily concerned with the even more variegated "languages" used in more complex social situations ("social" in the every day sense of the term). It has involved description, decipherment, and efforts to detect and formulate the general rules, the "grammar and syntax," of a multiplicity of signal systems. There have been surveys and comparisons of the signals of different groups of animals (*e.g.*, Tembrock, 1959; Lanyon and Tavolga, 1960; Busnel, 1963; Sebeok, 1968), somewhat abstract discussion of theory (*e.g.*, W. J. Smith, 1965 and 1969; Moynihan, 1970; Cullen, 1972; Mackay, 1972), and detailed accounts of particular systems, ranging from the pheromones of insects (*e.g.*, the work of E. O. Wilson and his col-

leagues) through bird "song" (*e.g.*, Thorpe, 1961; Hinde, 1969) to the non-verbal movements and expressions of children and adults in contemporary western and other human societies (*e.g.*, Goffman, 1971; Blurton Jones, 1967 and 1972; Argyle, 1972; Eibl-Eibesfeldt, 1972). These studies may have implications for related fields. They have, for instance, at least made available to "real" linguists such as Chomsky, Lenneberg, etc., some useful background material and evolutionary perspective.

3. However valuable such works may be, they would appear to be diversions from the classical behavioral point of view. Most active students are proceeding, and probably will continue for the foreseeable future, in one or the other of two different directions, two new mainstreams. Those who are preoccupied with immediate causes are going into physiology in earnest, laboratory research on hormones, nerve cells, receptor organs, at the deepest or lowest, even molecular, level. I cannot say anything about this. Results are obviously flowing in, but the subject is complex and not my major interest and I am not competent to discuss it.

4. Ethologists who are more concerned with ultimate causes are exploring connections or interfaces among behavior, ecology, and evolution.

This has been my own preference. I may, therefore, be able to illustrate some of the positive virtues and negative drawbacks of the approach by citing particular cases from my own experience. In recent years, I have been engaged in observation and analysis of three groups of animals, cephalopods, New World primates, and passerine birds (and some "near passerines" such as hummingbirds), in the field in natural or semi-natural conditions.

EXAMPLES

1. I was attracted to cephalopods for several reasons. They provide remarkable examples of evolutionary and ecological convergence. Beginning with a molluscan body plan, they have acquired large size, good eyes, large brains, and (in many species) active and predatory habits. They have become similar to many fishes and other aquatic vertebrates in these respects. (The convergence is discussed at length *in* Packard, 1972.) They have also evolved unique or peculiar characters such as distinctive methods of buoyancy control, color changes, and jet propulsion. Combinations of some of these features have finally

allowed them to invade the laboratory, to serve the neurophysi-
ologist. I would say, without being an expert, that some of the
operations of their central nervous systems and their handling of
visual information must be better known than the corresponding
processes of any other animals with the possible exception of
man. See, for instance, Young (1964 and 1972), Wells (1962),
and the many papers of Sutherland and his co-workers.

In these circumstances, it is noteworthy that the social be-
havior of cephalopods has not been studied in anything like the
detail that might, off-hand, have been expected. (There are
technical reasons for this comparative neglect. Most cephalopods
do not live long in captivity and/or are difficult to follow in the
field.) Such work as has been done on the subject has been
unevenly distributed. The great majority of living species of the
class can be assigned to one or the other of three diversified and
flourishing orders. Using the terminology of Jeletzky (1966),
these may be called Teuthida (including the squids), Sepiida
(cuttlefishes and their relatives), and Octopida (octopi and
argonauts). There are more or less lengthy published accounts
of the social behavior in the laboratory of the common European
cuttlefish, *Sepia officinalis* (L. Tinbergen, 1939; Holmes, 1940),
and the common octopus, *Octopus vulgaris* (*e.g.*, Packard and
Sanders, 1971; Wells and Wells, 1972), but relatively little on
other species, only bits and pieces on some reactions of a few
other sepiids and octopi and several kinds of squids, mostly
Loligo spp., in the laboratory or in the field (see references *in*
Lane, 1957, and Moynihan, in press b).

I was delighted, therefore, to encounter a species of squid,
Sepioteuthis sepioidea, in the San Blas Island region of the At-
lantic coast of Panama which is quite unusually easy to observe
in the wild under natural conditions. Mr. Arcadio Rodaniche
and I seized the opportunity to look at its social behavior. We
have now been observing it at monthly intervals for over two
years.

The species occurs inshore in moderately or very shallow
waters over turtle grass and coral. It is often extremely abun-
dant. It is a true squid, but rather cuttlefish-like in shape,
adapted for "hovering," and much less rapidly or continuously
mobile than most other squids (see also Boycott, 1965). It is
both predator, eating small fishes and crustaceans, and prey,
being eaten by large fishes such as barracuda and snappers (and
perhaps many other animals, including birds, Brown Pelicans,
etc.). Individuals of the species tend to scatter singly or in pairs

or trios to hunt more or less actively at night, but they congregate in large groups in the daytime to wait for prey to come to them. The daytime groups may be almost completely stationary for long (several hour) periods. Even when they are less sluggish, they tend to keep within rather small territories or home ranges. Groups are easily habituated to the presence of human observers. (In fact, one of the few technical problems of working with the species is to keep from getting too close to retain perspective and an overall view.) Individuals in groups are not shy about performing a variety of elaborate social reactions, including the full range of "courtship" and copulatory patterns, before human observers. Thus, they have provided us with a superfluity of data.

What have been the results?

In one sense, they have been disappointingly conventional. The social behavior of *Sepioteuthis* is essentially vertebrate-like in basic articulation and organization. There do not seem to be any general principles of molluscan behavior apart from those shared by most other complex animals of other phyla. But this squid does exhibit or illustrate a whole series of interesting special adaptations which may be correlated with, causally related to, one significant aspect of its ecology — and many of which may also be characteristic of other cephalopods and for the same reasons.

S. sepioidea populations are highly structured. Not only do individuals repeatedly leave and rejoin groups, but even the groups are formed of sub-groups which may be separate at some times, with obvious hostility and territorial defense among themselves, yet completely integrated at other times. There also are size and (presumably) age classes that assort themselves in particular spatial arrangements according to particular temporal and physical circumstances. The system is both intricate and flexible, apparently at least as much so as those of such mammalian carnivores as lions, African hunting dogs, and Spotted Hyenas.

The system is mediated by signals, both ritualized (mostly displays) and unritualized. As far as we can tell, all the signals are visual. (Cephalopods seem to be deaf, and we did not detect, see, any indications of the use of pheromones or other means of olfactory communication.) The visual signals include postures and movements and many color changes. The number of ritualized patterns is quite high. The basic components of the ritualized repertory may not be more numerous than the corresponding elements in the repertories of certain birds and

fishes (see Moynihan, 1970), but they can be combined and recombined almost endlessly. It is not uncommon to see an animal adopt two or three, even four or five, color patterns simultaneously, each color on a particular part of the body, while performing a series of movements, especially of the fins or arms, in very rapid succession. The effect is Protean. A squid is quite able to transmit a variety of different signals in different directions to different receivers, different kinds of onlookers, all at nearly or completely the same times. As visual signal systems go, the cephalopod versions must be unique in their combinations of speed and diversity or multiplicity and perhaps efficiency.

Comparison of the known patterns of *Sepioteuthis, Sepia, Octopus,* and some other cephalopods has revealed some sugges-tive similarities and contrasts. Some displays are very distinct, obviously not homologous, in the different species. Others are very similar. Some of these are relatively simple. They may well have become ritualized independently in each of the phyletic lines. But at least four major displays are both extremely com-plex, exaggerated, and "unexpected," and yet strikingly similar in many details (of causation and function as well as form) in the various species. These displays would appear to have be-come ritualized before the lines diverged from one another. As the divergence must have occurred well before the end of the Mesozoic, perhaps most probably in the Late Triassic, the pat-terns are not only old but also have been remarkably conservative during evolution. To my knowledge, they have been more con-servative than any patterns of other groups so far recorded in the literature. One of the reasons why some or all of them have been stable is apparent when they are compared with the other dis-plays of the same species that have changed more considerably or developed more recently. The latter tend to be shown to only a few individuals or types of individuals. The conservative sig-nals, on the other hand, are designed to influence a great number and diversity of receivers, different age, size, and sex classes of the same species and/or individuals of other species, especially potential predators. This may be a general rule, applicable to most animals. All other things being equal, the more widely reflected or broadcast a signal, the more conservative it will be, the more narrowly reflected or broadcast, the more likely it is to be changeable in evolutionary time.

The role of predation should be emphasized in connection with cephalopods. There is good evidence (see Moynihan, in press c) that several or many of the living members of the class

are favorite prey of marine birds and mammals almost throughout the seas and oceans of the world. They must, therefore, be themselves enormously abundant in many areas. (Common as it is, *Sepioteuthis* has a fairly restricted distribution in the tropical Atlantic. Other squids must have larger populations. The total numbers of cephalopods in any given area are difficult to estimate precisely, as many species are nocturnal and most are difficult to catch with the traditional gear of marine biologists, but the birds and mammals probably are more efficient collectors.) There also is evidence that the enormous biomass of cephalopods is divided among fewer "packets," *i.e.*, species, than is that of their nearest competitors, the marine fishes. This could be both cause and consequence of their relatively greater attraction for predators.

It may be assumed that many of the extinct cephalopods exhibited some or all of the demographic and ecological characteristics of their living relatives. If so, it seems likely that predation pressure could have been the major impulse for a series of evolutionary events. Some of the probable steps can be listed briefly and crudely. The ancestors of the majority of living cephalopods presumably reduced, internalized, and in some cases lost, their originally external shells to gain greater maneuverability and powers of escape. This "freed" their skin for other uses, including the elaboration of color change mechanisms. The development of gregarious habits may well have been another (even earlier?) anti-predator adaptation (Brock and Riffenburgh, 1960). The habit of living in groups puts a premium upon the development of complex signal systems. For vulnerable marine animals, a visual communication system has definite advantages. (Visual signals can be turned off instantaneously whenever necessary or desirable, unlike olfactory cues, and they are perhaps less apt to be noticed at a distance by dangerous receivers than are acoustic signals, especially in murky waters or around reefs or vegetation. And, of course, short range signals are perfectly adequate as long as the animals are close together.) Once the skin has become specialized for color changes, it probably is not easily transformed for other purposes such as the development of new kinds of armor or spines. This restricts the choice of further anti-predator adaptations. It has already been mentioned that whatever displays may have to be shown to potential predators are conservative. As many or most of these patterns are also used in intraspecific encounters, they may tend to impede fundamental changes in the type, although certainly

not the details, of the signal system as a whole. Other char-
acters of cephalopods such as their rapid growth, relatively short
life spans, special arrangements and care of eggs (see, for in-
stance, Packard, *op. cit.,* and Wells, *op. cit.*), and even their
preference for reproducing only once in a lifetime, in "big bangs"
(Gadgil and Bossert, 1970), could also be explained as responses
to intense predation. (And the need to synchronize reproductive
moods in a hurry, without much time for trial and error, must
add another premium for both gregariousness and the elabora-
tion of signals.)

The series is an illustration of some of the ways in which
ecology and behavior can interact to determine the course of
evolution, each step opening up some possibilities and foreclosing
others.

2. The New World primates are a variegated family of mon-
keys of some 11 to 13 genera and many species. I have observed
representatives of all the genera at irregular intervals over 15
years. Some species have been observed only in captivity, at the
field station on Barro Colorado Island and in zoos in Washing-
ton, London, Paris, and Amsterdam; but many others have been
studied at considerable length in the wild, in the central part of
the isthmus of Panamá, to the west in the province of Chiriquí,
and to the south in the upper part of the Amazon basin, in the
Caquetá and Putumayo regions of Colombia.

For most biologists, the primary significance of the American
monkeys is that they represent a wide and independent adaptive
radiation. They have occupied most of the habitats available to
primates. In this respect, they are more or less strictly equivalent
to the two other radiations of modern primates, the (Recent and
Pleistocene) lemuroids of Madagascar, and the so-called Old
World monkeys and apes, the "Catarrhini," of tropical Asia and
Africa and some adjacent areas, of which man is a specialized
offshoot. The New World forms may thus provide a useful
check to hypothesis and speculation about the evolution of pri-
mates in general and man in particular. I should also like to
claim that they are interesting in themselves.

They range from very small (the Pigmy Marmosets of the
genus or sub-genus *Cebuella*) to moderately large (the howlers,
Alouatta, and the spider monkeys, *Ateles*). They show a great
diversity of types of locomotion, from squirrel-like scrambling
and/or vertical clinging and leaping among the marmosets and
tamarins (*Saguinus, Leontideus, Callimico,* and *Callithrix* in
addition to *Cebuella*), through quadrupedal "springing," walk-

ing and pacing in such forms as *Saimiri* and *Cebus,* to brachiation or semi-brachiation with the supplementary use of a prehensile tail in *Ateles.* (The classification and details of locomotion are discussed *in* Erikson, 1963, and Napier and Walker, 1967.) At least two species of *Cebus, capucinus* and *apella,* come down to the ground with appreciable frequency. All or most of the species of other genera are thoroughly arboreal. One genus, *Aotus,* is nocturnal; the rest are diurnal. They all tend to be nearly omnivorous on occasion; but most of the smaller forms, many of the tamarins and probably the marmosets of the genus *Callithrix,* seem to prefer insects whenever they can get them, while some of the larger forms are essentially herbivorous, taking various assortments of fruits of particular kinds and ages, as well as buds and leaves and even twigs and bark. At least one form, *Cebuella,* has specialized in sap-sucking. (The sap-sucking is described *in* Moynihan, in press d. The best general accounts of more conventional feeding habits and régimes, unfortunately limited to the Panamanian species, are *in* Hladik and Hladik, 1969, and Hladik *et al.,* 1971.)

In the course of my own studies, I have attempted to discover and analyze the social behavior and structures of different species and combinations of species, to determine how such complexes are held together (or apart as the case may be), and to identify some of the selective forces involved, to tie the observed behavior to particular aspects of ecology. The results summarized below are taken from Moynihan (in press a); this book also lists references to papers and unpublished notes of other workers.

Two extreme types of intraspecific social organization can be recognized without much difficulty: the restricted "nuclear" family group and the large band. The former seems to be the basic social unit of *Aotus, Callimico;* two species of *Callicebus, moloch* and *torquatus;* and, in some circumstances, *Pithecia monacha.* Bands are characteristic of *Pithecia melanocephala, Alouatta villosa, Alouatta caraya, Lagothrix, Saimiri,* and some or all forms of *Cebus* and *Ateles.* As might be expected, there are intermediate conditions, complications, and exceptions. One type of intermediate is the "extended" family of some species of *Saguinus,* e.g., *fuscicollis, graellsi, midas,* and *Cebuella* and probably many other marmosets. Intermediates can also be flexible, intermittent or recurring. Small families of some species may join one another in some circumstances. It also is normal or usual for neighboring small families of most species to perform

certain responses, *e.g.,* anti-predator reactions, in common. (This is evidence that they do form a real social community.) Conversely, large bands may split up into smaller sub-groups temporarily, or reveal traces of sub-group organization within the bands without actual splitting. This appears to be most common in *Saimiri* and some form of *Ateles*. (The sub-groups are not usually families but rather cephalopod-like age and sex classes.)

The adaptive value of such variance is surprisingly obscure. It seems to be characteristic of American monkeys that there is little general correspondence between basic types of intraspecific organization and either habitat or food preferences. There are species that live in bands and species that live in small family groups among the primarily or exclusively vegetarian forms. There also are both kinds of species, or at least forms that usually live in bands and forms that live in extended family groups, among the animals that prefer insect food when available. The proportions of highly to poorly gregarious species and individuals are much the same in many of the stages of succession from young second-growth scrub to mature forest in many areas. Perhaps even more remarkable, density of populations also appears to be largely irrelevant in this connection (if not for other aspects of social behavior — see below). Both *Callicebus moloch* and *Saimira* usually are abundant and concentrated wherever they occur. They are concentrated in different ways, but the average number of individuals per unit of time and area may be high in both cases. Both *Aotus* and *Cebus albifrons* can be described as dispersed. The *albifrons* occur in rather large bands, but the bands themselves are scattered.

These facts would suggest that almost any type of social organization can permit or facilitate almost any kind of exploitation of the environment within the range of niches occupied by American monkeys at the present time. Presumably, because most of them are more "generalists" than "specialists," they have been able to choose among alternative strategies to achieve similar ends.

Much more restricted are the modalities or techniques by which particular social systems are maintained. The ritualized signal systems of these animals are not only adaptive but are quite obviously so, down to the finest details. They include visual, acoustic, olfactory, and tactile patterns (Moynihan, 1967). Of these, the visual and acoustic seem to be usually most important. The basic elements, the deep structures, of the repertory of sounds may be nearly identical in all species, with the possible

or probable exception of *Alouatta*. It is not difficult to trace homologies among most of the vocalizations of most of the species, and much of the information encoded is almost uniform or strictly equivalent throughout. The forms and frequencies of particular patterns are, however, very different in different species. The differences seem to depend upon the distances over which sound usually need to be transmitted, the carrying properties of the medium (the numbers and kinds of obstructions likely to be encountered), and the presence or absence of other possible sources of relevant information, features of the external and/or social circumstances and other types of signals. In fact, this means that both the physical forms of the patterns and the methods of encoding information are closely correlated with social structure, density of population, activity rhythms, and density of vegetation, as well as vulnerability to predation and diversity of appropriate receivers. The ritualized visual signals are more heterogeneous but equally easy to explain in terms of the same factors.

Some New World primates are involved in, or are the foci of, specialized and stereotyped interspecific social reactions. Such reactions may take either positive or negative forms, "friendly" joining and following or hostile fighting or avoidance. They may occur among two or more species of monkeys and/or between monkeys and other animals such as squirrels (*Sciurus granatensis*, *S. variegatoides*, *Microsciurus* sp.), birds of prey such as *Harpagus bidentatus* and *Leucopternis albicollis* (these small hawks do not attack the monkeys themselves, but rather take the arthropods, lizards, etc., flushed by them), and even flycatchers (*e.g.*, *Myiozetetes*, *Tyrannulus*, *Lagatus*, *Elaenia*, *Megarynchus*). The combinations of positive and negative responses can be complex, and the interspecific relations of a single species may be different in different areas. It is possible, nevertheless, to detect certain general rules or trends.

There are apparent correlations among interspecific bonds, feeding habits, and territorial behavior. The monkeys that are most likely to mingle with other species are forms such as *Callicebus moloch* and *Alouatta villosa*. They are vegetarian, taking items such as leaves, buds, and berries that are abundant and evenly distributed, and have small territories or large territories through which they move slowly. Individuals and groups of these species seldom find themselves in situations with which they are not thoroughly familiar or have not had time to inspect carefully beforehand. Conversely, the establishment of friendly

interspecific bonds is characteristic of such forms as *Saimiri*, *Cebus apella*, and *Ateles paniscus s.l.* They are omnivorous or preferentially insectivorous or feed on plant materials that are dispersed or distributed in irregular clumps. They tend to have large territories through which they move rapidly. They must be precipitated into unfamiliar situations rather frequently. They must also, therefore, have more need of extra companions of the same or other species, to act as scouts or sentinels, than do species of more sedentary or cautious habits.

On logical grounds, one would suppose that the various kinds of interspecific social behavior should be adjusted to intensities of competition[1] as well as particular ecological facies. It would be expected that species that do not compete at all, or compete as little as may be feasible for animals that occur in the same areas, would usually tend to ignore one another. There are many apparent examples of such behavior among the New World primates. It would also be expected that species that compete very strongly would tend to exclude one another from wide areas and entire regions. Again there are apparent examples among the American monkeys.

Presumably either of these extreme types of interspecific behavior can be transformed into the other in the course of time. It would be interesting to know the intermediate stages. Data from observations of the New World primates and their associates would suggest that the following progression (quoted from Moynihan, in press a) may be common as intensity of competition increases: "When competition becomes slightly more than minimal, the species will tend to ignore one another in most circumstances but will exhibit overt and active hostility toward one another occasionally. (If it is only desirable or necessary to drive off rivals infrequently, it may be worth taking the risk of fighting.) When competition is stronger, it may be advantageous for the competitors to join up with one another. (If you can't lick 'em . . .) When competition becomes stronger yet, it may become imperative to avoid one another. First by avoiding personal encounters while still ranging over the same areas at much

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[1] I am employing such terms as "complete" and "competition" in the broadest possible sense. Two animals are considered to be competing with one another whenever one preoccupies, permanently or temporarily, any resource that would otherwise be likely to be used by the other. Among primates and birds, competition for preferred observation posts, singing perches, safe sleeping quarters, etc., may be quite as important as competition for food.

the same times. Then by claiming exclusive territories or by elaborating some form of temporal segregation. (Segregation by differential timing may have peculiar advantages, but it can only work when the species involved are not too numerous.) From the claiming of exclusive territories, there may be no more than a small step to complete allopatry. It seems very probable that the process can also go in the opposite direction, through the same stages but in reverse order, and that the direction of change can be reversed repeatedly, with or without reaching the extreme conditions at either end."

3. Most of my recent work on birds has been conducted in the Andes.

The higher reaches of these mountains provide a wealth of material for students of biogeography. They include a large series of habitats and biotas that differ from those of the surrounding lowlands in several respects (*e.g.*, temperature, endemic species). The northern part of the Andes is extremely complex in structure, with separate cordilleras, chains of mountains, and a scattering of single peaks and massifs. The central and southern parts are simpler, more unified in general or overall form, but still varied in details of terrain and climate. As a result, many of the higher altitude habitats and biotas are distributed in patches, partly or wholly isolated from one another. They are essentially insular. They differ from oceanic islands, however, in not being impoverished. The higher Andes have "complete" or "balanced" floras and faunas. They are inhabited by many kinds of organisms which have occupied most of the obvious niches or ecological roles, exploited most of the available opportunities. They are, therefore, ideal for analyses of some aspects of insular evolution. The effects of isolation and adaptations to facilitate or impede invasions can be studied *per se,* quite apart from the possible distortions of "accidental" barriers or "sweepstake" phenomena.

I have concentrated upon interspecific behavior among two groups of species of a particular "life zone." Observations were begun in 1959 and have continued off and on until the present. The results are being analyzed and written up. Many details remain to be settled, but the general sense of the bulk of the data is clear.

The life zone is the one that Chapman (1917 and 1926) called "humid temperate." The term is perhaps misleading — "cold humid tropical" might be more suitable (see comments *in* Moynihan, 1971). The zone is best developed around 2800–

3300 m in most areas. Its natural vegetation would be more or less dense forest and "alpine" scrub (Weber, 1969). Some of this survives apparently intact. The rest has been replaced by secondary bush, gardens, hedges, crop fields, pastures, etc. Fortunately, substantial numbers of the native birds have been able to occupy and even flourish in some (the lusher) of these man-made habitats. They are still easily observable. The distribution of the zone is eccentric within the Andes. It must cover almost the whole of the northern Andes at appropriate elevations, *i.e.*, it is scattered among islands, most of which are small, a few of which are large but long and narrow. It is much broader and more nearly continuous in the central Andes, in all or most of central Ecuador and northern Peru. It becomes progressively narrower toward the south, even though the Andes themselves remain broad. The apparent discrepancy is due both to the relief of the mountains and the nature of the prevailing wind systems (briefly summarized *in* Murphy, 1936). Rain falls off at an unequal rate. The principal southern extension of the zone is along the eastern slope of the chain, down into central Bolivia. It is dissected by the deep valleys of rivers flowing to the Amazon. In effect, the southern extremities are a series of narrowly linked narrow peninsulas.

My own observations have ranged from the Sierra de Mérida in Venezuela and the Sierra Nevada de Santa Marta in northern Colombia down through central and southern Colombia, Ecuador, and Peru to northern Bolivia, the Yungas of La Paz, at altitudes between 2400 and 3700 m. This is nearly the full length of the cold humid tropical zone, with the addition of some fringe areas of adjacent zones.

One of the groups of species studied could be called the "*Diglossa* cluster." It includes six species or superspecies of the genus, flower-piercers, which may be called *carbonaria, lafresnayei, albilatera, baritula, cyanea,* and *coerulescens* (this is the nomenclautre and classification of Zimmer, 1929; Hellmayr, 1935; and de Schauensee, 1970 — Vuilleumier, 1969, suggests a slightly different arrangement, and other refinements are conceivable), as well as the conebill *Conirostrum cinereum* and some hummingbirds such as *Colibri coruscans, Aglaeactes cupripennis,* and *Ramphomicron microrhynchum.* All these birds are nectarivorous to a greater or lesser extent.

The other group includes many more species of different sub-families, families, and at least one more order. For want of a better name, I shall call it the "tanager cluster." It includes a

variety of closely related montane tanagers, mostly black and blue with touches of yellow, buff, or red, of such genera as *Anisognathus, Buthraupis,* and *Iridosornis* (and also the "Plush-capped Finch," *Catamblyrhynchus,* hardly distinguishable from *Iridosornis* in appearance or habitus in the field[1]); other tanagers of rather different stocks (*e.g., Chlorospingus, Cnemoscopus, Hemispingus, Chlorornis*); finches of the genus *Atlapetes;* some other conebills (especially *Conirostrum sitticolor* — see Moynihan, 1968); warblers of the very different genera *Myioborus* and *Basileuterus*[2]; a few flycatchers (*e.g., Uromyias* and *Megacerculus* spp.); the occasional hummingbird (*e.g., Ensifera* and *Coeligena*); a few woodpeckers (*e.g., Piculus rivolii* in Venezuela); and many furnariids and dendrocolaptids (*Margarornis, Synallaxis, Cranioleuca,* etc.). And at least one squirrel in the western cordillera of Colombia (*Sciurus granatensis* again!). The association includes frugivores (different species taking different fruits), insectivores (catching different insects in different ways), a new nectarivores, and many types with very mixed diets. Different species also prefer different levels of vegetation, from the highest tree-tops down to the ground.

The chief peculiarity of both clusters, the one that drew my attention, is that their members show pronounced *intraspecific* geographic variation in their *interspecific* behavior. More precisely, individuals of a single species or superspecies react very differently to individuals of other species in different regions (often the same other species in each of the regions). The variation affects different types of interspecific behavior in the two clusters, hostility in the *Diglossa* association and "friendliness" in the tanager association, but the trends are roughly parallel in both, although inverse and complicated by certain exceptions. The exceptions themselves are sometimes revealing.

The situation is roughly as follows:

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[1]The classification of the "New World nine-primaried songbirds" is in need of further revision. Some of the supposed families and subfamilies of the group appear to be polyphyletic in origin. Some of the genera currently assigned to one family may be more closely related, phylogenetically, to some of the genera assigned to other families than to other genera assigned to the same family. Terms such as "warbler," "tanager," and "finch" are little more than short-hand descriptive labels for certain ecological categories.

[2]In the case of these Andean birds, it seems probable that a revised scheme would place the Plush-capped Finch in the same tribe as the tanagers it so much resembles, and also link *Basileuterus* to *Hemispingus* rather than to *Myioborus.*

Many members of the tanager cluster extend throughout all or
most of the cold humid tropical zone. All show tendencies to
form or join mixed species flocks in some areas and regions (this
is the prescriptive reason why they have been assigned to the
cluster). In general, individuals of the same species behave in
similar ways in the northern and southern extremities of the zone,
but very differently in the central part. They show a high degree
of interspecific gregariousness in the western and central cordil-
leras of Colombia (the western cordillera is always extremely
northern, "far out," in the behavior of its inhabitants — see also
below). In these regions, the birds occur in mixed flocks most
of the time, and most of the flocks are large, cohesive, complex
in structure, and stable (maintained for hours on end and often
re-formed on successive days). In the eastern cordillera of Co-
lombia and the Sierra de Mérida, the birds still show a con-
siderable amount of interspecific gregariousness, but mixed flocks
are formed somewhat less frequently and tend to be smaller,
looser, and simpler in structure on the average (the decline may
be more evident in the eastern cordillera than in Venezuela).
In central Ecuador and central and northern Peru, interspecific
gregariousness is slight. In fact, quite absent in some localities.
Even when and where mixed flocks *are* formed, they are always
small and simple, and usually loose and sustained for only a few
minutes. The trend is reversed in southern Peru and northern
Bolivia. Mixed flocks become larger, more stable, cohesive, and
complex again (rather more so in Bolivia than in Peru, but never
as much so as in the western cordillera of Colombia).

It is obvious that the development of flocking depends upon
several factors. There are positive correlations among densities
of populations, thickness of vegetation, and frequency and elab-
oration of interspecific gregariousness within regions. But these
cannot account for the whole of the major geographic trends.
They do not explain the exceptions. There must be something
else involved. This would appear to be an "invasion" or "fron-
tier" effect. Interspecific gregariousness seems to go up with
exposure to, or anticipated number of, invasions from or into
other regions of the same life zone or an adjacent zone, the warm
or hot humid zone of lower elevations.

The western cordillera of Colombia is the least continuous of
the major chains of the Andes. Its patches of cold humid habi-
tats are comparatively small. The populations of these small
islands must include a relatively very high proportion of indi-
viduals near the frontiers of their patches and a low proportion

of individuals at the centers of patches, away from the frontiers. The same must be true of the populations of the narrow peninsulas of the zone in the far south. Birds on the frontiers must encounter strays from other zones and stray into other zones more often than do birds from the centers. It would seem that this is one of the causes of interspecific gregariousness. The evidence is somewhat restricted, but I think convincing. In central Ecuador, I worked along one transect from the top edge of cold humid forest and scrub down into the upper reaches of warm humid forest. Interspecific gregariousness is essentially nil in the higher part of the cold humid zone, but increases abruptly at the exact point where occasional strays from the warmer zone begin to appear with some appreciable, if still low, frequency. (The increase is "intrinsic." It is always apparent, whether or not strays are present at the moment.) The remarkably high degree of gregariousness of the birds of the central cordillera of Colombia, higher than would be expected of its not particularly northern or isolated position, may also be correlated with the fact that it is exposed to invasions from the nearby chains on either side as well as from the immediately adjacent lowlands.

What is the functional significance of this apparent connection of interspecific gregariousness with frontiers, strays, and invasions? The advantages of mixed flocking from the point of view of a straying bird in an unfamiliar area are obvious, and much the same as in the monkeys cited above. By associating with experienced local individuals, a stray may be able to discover and identify food and/or danger relatively rapidly. The advantages for the "hosts" of a stranger are more problematical. Of course, they are acquiring a companion who may be of use in various ways. They are also encouraging or tolerating a competitor. Perhaps one of the reasons that they do so is that they may become strangers in their turns. Some of them must also stray into adjacent life zones, where they will also need the help of local inhabitants. It may be difficult for an animal to join and follow strangers without also developing some tendency to allow itself to be joined and followed by strangers. (The roles of joiner and joined are easily distinguishable in some areas such as parts of Panama — see, for instance, Moynihan, 1962a — but they are less clearly distinct in these Andean flocks. In any case, both roles often reflect similar states of mind.) It seems to be characteristic of most animals that they cannot, at least do not, support very great qualitative differences in kind of social responses. A species that is comparatively aggressive in one class of social

encounters also tends to be aggressive in other encounters. Similarly, a species that is gregarious in some circumstances usually tends to be gregarious in other circumstances.

This "extrapolation" may have been favored in Andean birds because the boundaries of their life zones have been fluctuating, repeatedly shifting back and forth in recent geological history (see Simpson-Vuilleumier, 1971). Many of the birds of the cold humid zone must have had to invade new areas, and cope with invaders from other areas, again and again in response to secular climatic changes, quite apart from or in addition to the normal straying that would have occurred even if the frontiers had been fixed and permanent.

The species of the *Diglossa* cluster show another contrast between individuals of the central part of the cold humid zone and those of the northern and southern extremities of the zone. Some aspects of their interactions in central Ecuador have been described *in* Moynihan (1963). Each of the local species has its own, partly unique, series of ecological preferences, but the ranges of most species are broadly overlapping. The territories of individuals of different species are often completely overlapping. Individuals of different species may use the same perches, move along the same pathways, feed in the same places on the same types of foods. But they almost never do so simultaneously. They are almost always kept a few meters apart, at any given instant of time, by some avoidance mechanisms. There is also mutual inhibition of "Song" among individuals of different species of *Diglossa* and *Conirostrum cinereum*, although not among individuals of the same species. The whole thing can be summed up as rigid and continuous social segregation. In the western cordillera of Colombia and in northern Bolivia, on the other hand, many of the species are separated microgeographically, each largely or completely confined to a particular facies of habitat slightly different from the facies of all or most of the others. This may be due to fighting. On the rare occasions when individuals of different species that are usually separated do happen to come together, they usually fight, actually attack, one another. There is no visible avoidance mechanism. Thus, the microgreographical segregation may be encouraged or imposed by reactions among individuals but it is not continuously social in the same way as in central Ecuador. Conditions are more or less intermediate in the Sierra de Mérida, the eastern *and* central cordilleras of Colombia, and many areas of Peru, with all com-

binations of partial overlaps, incomplete avoidance and inhibition, and more frequent and prolonged overt disputing.

The variations of the birds of the *Diglossa* cluster are also correlated with factors such as density of vegetation and interspecific competition. They do not, however, include frontier effects. They would seem to be more concerned with size of local populations and competition within regions rather than invasions by strays from without (*Diglossa* individuals are very sedentary). Individuals of the small northern and southern populations may hope to fight off all or most of their not very numerous competitors with relative ease. Individuals of the larger central population probably could not fight off their more numerous competitors without exhausting themselves in the process or taking unacceptable risks of physical injury.

It will be noticed that different adaptations for coping with interspecific competition may tend to produce different diversity gradients in the two assciations. In the *Diglossa* cluster, species diversity at any given point is least at the extremities and probably greatest at the center of the cold humid zone. In the tanager cluster, species diversity must often be greatest at particular points in the extremities and least at the center.

COMMENTS

The sorts of work cited above are perhaps typical of a contemporary approach to ethology. I should hope that they would suggest certain conclusions about studies of behavior and the relationships of such studies to analyses of evolutionary processes.

Beginning with the purely ethological aspects, it seems evident that causation is the crucial problem. Studies of ultimate causes, natural selection, seem to be proceeding fairly well. At least, there are no theoretical or basic methodological difficulties involved. Studies of proximate causes, physiology, may also be making progress, perhaps more rapid and exciting progress. But there is very little contact between the two lines of investigation, least of all when vertebrates provide the working material. Doubtless, there will be a new and sophisticated synthesis of the two approaches at some date in the future. I do not expect to see it in my own (research) life time. I should also imagine that, when it comes, it will be largely due to an expansion of concern and efforts by physiologists. They would seem to be in a better practical position to develop the necessary techniques than are the field-oriented "natural historians."

Meanwhile, there is still a lot that the ethologist can do for for the evolutionist.

Behavioral information can help to illuminate the evolution of particular groups of animals. They have, for instance, increased our knowledge of the phylogenies of many vertebrates such as ducks and geese (Lorenz, 1941; Delacour and Mayr, 1945; Johnsgard, 1965), gulls and terns and their relatives (*e.g.*, Moynihan, 1962b), and cichlid fishes (*e.g.*, Baerends and Baerends, *op. cit.*). As taxonomic characters, however, behavior patterns are no more and no less valuable than any other characters. They may be more useful in some cases than in others, more useful than other features in some groups, less useful in other groups. They should continue to be considered, to be taken fully into account, in systematic studies. But I would suggest that they can make a more significant contribution to the analysis of evolution by providing concrete, immediate, information to help explain certain ecological phenomena, developments, and interactions which are themselves among the causes of evolutionary changes.

A substantial proportion of current and recent ecological research has been devoted to such matters as competition, coexistence, partitioning of resources, invasions of new areas and habitats, replacement, and extinction (see the works of Hutchinson, MacArthur, Wilson, and others). There has been a stimulating sequence of papers with models and diagrams, mathematical formulae and other elaborations of symbolic logic, to describe and summarize the results of interactions among individuals and species at present, as they probably were in the past, and as they may be expected to be in the future and always. What seems to me to have been lacking in many or most of these discussions is attention to some of the details of the ongoing processes as well as their end products, how and why they actually work in fact and in nature, the mechanics by which the final results are achieved. A great many questions have been left hanging in air. What do individuals of the same or different species really *do* when they come face-to-face with one another? Or when they occur in the same areas without necessarily encountering one another directly? What are the forms of competition? Who moves where, and why and when? How are specific resources found, used, preoccupied, defended? What are the relevant clues? How does replacement occur on a day-to-day or year-to-year time scale? What are the adaptations which permit or facilitate supplants and invasions? How are these

adaptations used in life and why are they effective? Why are some adaptations more effective than others that could have been used instead? Is there any consistent relation between size of area inhabited and probability of success? Are there some species that are really specialists in competition? If so, why? And how do they manage it?

These are the kinds of questions which behaviorists should be able to answer, in whole or in part. I think that many behaviorists are trying to find the answers now. I hope and expect that they will continue to do so.

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